

## **The Aspidogastrea**

**Klaus Rohde, Zoology, School of Environmental and Rural Science, University of New England, Armidale NSW 2350, Australia [krohde@une.edu.au](mailto:krohde@une.edu.au)**

### **Introduction**

Trematodes (flukes) one of the largest groups of helminths (parasitic worms) with thousands of species, comprise the Digenea and Aspidogastrea. Many species, all belonging to the Digenea, have great economic or medical importance. The Aspidogastrea (=Aspidobothria, Aspidobothrea), in contrast, are a very small group of trematodes with around 60 species, none of them of practical importance. But they have found great interest because of their unique structure, their simple life cycles which may well be the most ‘primitive’ ones among the trematodes, and the extraordinarily complex sensory/nervous systems found in some species.

Extensive lists of references of the group were given by Rohde (1999)

<http://tolweb.org/Amphilinidea> and Alves et al. (2015).

### **Main characteristics**

Larvae always have a posterior sucker, and an anterior so-called “pseudo- or false sucker,” which is not separated from the surrounding tissue by a genuine connective tissue sheath, may also be present (Figure 1).

<Figure 1 here>

Adults do not have a posterior or ventral sucker, but an adhesive (ventral) disk consisting of transverse grooves (rugae), a single row of well separated small suckers (suckerlets) or three to four rows of alveoli (suckerlets) on a ventral disk (see Figures 2, 3, and 4), and – although hosts include vertebrates and molluscs – there is no multiplication of larval stages in the mollusc, i.e. a single egg produces a single adult.

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All aspidogastreans are hermaphroditic, i.e. the adults possess male as well as female reproductive systems. This is demonstrated below by the example of *Multicotyle purvisi* from the stomach and intestine of freshwater turtles in Southeast Asia. It reaches a length of about 10 mm and contains both a fully mature male as well as a fully mature and gravid female reproductive system (Figure 5).

<Figure 5 here>

Unique feature of the Aspidogastrea include a septate oviduct (i.e. the oviduct carrying the egg cells from the ovary has a number of concentric constrictions), and the marginal bodies, which were long considered to be glandular in nature but are in fact secretory organs (Rohde, 1971) (Figures 6 and 7).

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<Figure 7 here>

### **Life cycles**

The life cycles of several species have been worked out. Based on the knowledge available to date we can distinguish two kinds: in one type, the entire life cycle can be completed in molluscs, although vertebrates may act as facultative (not obligate) hosts, in the other, both a mollusc and a vertebrate are required for completion of the life cycle. An example of the first kind is *Aspidogaster conchicola*, whose life cycle has been studied by many authors beginning in the 19th century (references in Rohde, 1972, 1999) (Figure 8).

<Figure 8 here>

An example of the second kind of life cycle is *Lobatostoma manteri* from the small intestine of the marine teleost fish *Trachinotus blochi* (Rohde, 1973) (Figures 9 and 10).

<Figure 9 here>

At Heron Island on the Great Barrier Reef, only juvenile *Trachinotus* (a few centimeters long) were found to be infected. They crush the very thick-shelled snails between their well developed pharyngeal plates (Figure 10).

<Figure 10 here>

Larvae hatch in the stomach of the snails but move into the digestive gland where they grow up (Figure 11).

<Figure 11 here>

Like *Lobatostoma manteri*, *Multicotyle purvisi* (Figure 5) also needs a mollusc and vertebrate host for the completion of its life cycle. However, infection of the mollusc is not by an egg that is ingested, but by a larva that hatches in freshwater, swims for hours by means of its 10 ciliary tufts (Figure 12) and supported by a flotation mechanism, a thick sheath of so-called microfila (Figures 12 and 13). Larvae are inhaled by snails, and migrate into the kidneys where they grow to the stage infective to turtle (Rohde, 1971a).

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<Figure 13 here>

It is possible that other species of aspidogastreaans have more complex life cycles. Thus, larvae of *Stichocotyle nephropis*, adults of which infect elasmobranchs, were found encapsulated in the intestinal wall of lobsters, and immature *Multicalyx*, adults of which infect holocephalans and elasmobranchs, have been recorded from the intestine of teleost fish. This suggests that, in

addition to the intermediate and final hosts, a further host acting as a transport host (i.e., a host containing immature stages which do not develop in it), may be involved.

In all species of Aspidogastrea that have been studied, the posterior sucker of the larva is transformed into the adhesive disk: in *Rugogaster*, for example, the rugae are formed by the posterior wall of the sucker (Rohde and Watson, 1992a), in species of *Lobatostoma* and *Multicotyle*, among others, alveoli are formed within the sucker. Detailed studies of *Stichocotyle* have not been made.

### **Taxonomy and phylogeny**

About 60 species of aspidogastreans in 13 genera have been described. There has been some controversy about the relationships of the various genera of aspidogastreans, but according to the prevailing view, four families are distinguished as follows (Rohde, 2002):

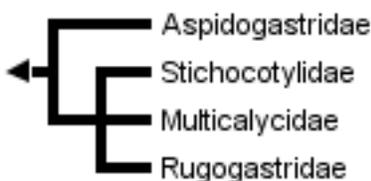
- 1) Rugogastridae (two caeca, single row of transverse rugae) comprising a single genus *Rugogaster* with two species from the rectal glands of holocephalan fishes;
- 2) Stichocotylidae (one caecum, single row of well separated suckerlets) with a single species, *Stichocotyle nephropis*, from the intestine of elasmobranchs;
- 3) Multicalycidae (one caecum, single ventral row of alveoli separated by transverse septa) with a single genus *Multicalyx* from the intestine of holocephalan fishes and elasmobranchs;
- 4) Aspidogastridae (one caecum, ventral disk with three or four rows of alveoli) with nine genera in three subfamilies from molluscs, turtles and teleost fishes;
  - 4a) Subfamily Rohdellinae (terminal part of male and female reproductive ducts united to form a hermaphroditic duct) with a single species *Rohdella siamensis* from freshwater teleosts;
  - 4b) Subfamily Cotylaspidinae (three rows of alveoli) with three genera, *Cotylogaster*, *Cotylaspis* and *Lissemysia* which differ in the number of testes (one or two) and the absence or presence of a

cirrus pouch;

4c) Subfamily Aspidogastrinae (four rows of alveoli) with six genera, *Multicotyle*, *Lobatostoma*, *Aspidogaster*, *Lophotaspis*, *Sychnocotyle* and *Neosychnocotyle*, which differ in the number of testes (one or two), the absence or presence of a cirrus pouch and the absence or presence of head lobes and/or papillae on the ventral disk.

Whereas the Aspidogastridae have an adhesive disk bearing three or four rows of alveoli and use teleosts/turtles as hosts, all the other families share the characters (synapomorphies) rugae or a single row of deep suckers/alveoli, as well as the use of elasmobranchs/holocephalans as hosts.

Gibson and Chinabut (1984) therefore distinguished two orders, the Aspidogastrida with the single family Aspidogastridae, and the Stichocotylida with the other families. DNA-studies on the relationship of the families with each other have not been made; the following diagram illustrates the likely relationship of the aspidogastrea families with each other based on morphology and hosts:



The sister group of the Aspidogastrea is the very large group Digenea, with thousands of species and many families (e.g. Park et al., 2007). The ancestor of the Digenea split from the ancestor of the Aspidogastrea early in evolutionary history, probably more than 400 million years ago (Littlewood et al., 1999). Comparative studies using 18S rDNA (Littlewood et al., 1999), 28S rDNA (Litvaitis and Rohde, 1999), as well as extensive electron-microscopic studies (e.g. Ehlers, 1985, Littlewood et al., 1999), have demonstrated that the Trematoda (Aspidogastrea plus Digenea), the Eucestoda, Gyrocotylidea and Amphilinidea, as well as the

Polyopisthocotylea and Monopisthocotylea (commonly put in the Monogenea which - however - is not a monophyletic group, e.g. Littlewood, 2006), i.e. all the major groups of parasitic Platyhelminthes, have one common ancestor, i.e. form one monophylum, the so-called Neodermata (e.g. Ehlers, 1985; Rohde, 1997) also confirmed by later DNA –studies (e.g. Egger et al., 2015).

### **A countertrend to sacculinisation**

In discussing the question of directedness in evolution, The Nobel-prize winner Konrad Lorenz, one of the founders of the modern study of animal behavior (ethology), pointed out that, “from each already achieved stage of development evolution can go on in any direction whatever, blindly responding to every new selection pressure that turns up” (Lorenz, 1987). He illustrated this by the process of retrograde evolution in certain parasites, a process for which he coined the term “sacculinisation.” The term is derived from the parasitic crustacean *Sacculina*, which has typical free-living crustacean larvae with complex articulated appendages like for example crayfish. After infecting crabs, it matures and all the appendages disappear. What is left is a sac-like appendage (the “externa”) on the ventral side of the crab’s abdomen which contains the gonads, and a cancer-like growth in the interior of the crab which absorbs nutrients from the host. This “degenerate” evolution is common among parasitic crustaceans and certain snails.

### ***Increase in complexity***

However, parasitism does not always lead to reduction in complexity, on the contrary, it may have the opposite effect, as shown by the Aspidogastrea. Extensive light- and electron-microscopic studies of several species of Aspidogastrea, in particular *Lobatostoma manteri* and *Multicotyle purvisi*, have demonstrated an amazing variety of sensory receptors not only in the larva, but in the adult as well, some of them occurring in very large numbers. This variety of

receptors is as great or greater, and their number is considerably greater than in those related free-living flatworms, the turbellarians, which have been examined. Likewise, the nervous system of the Aspidogastrea examined shows greater complexity than that of turbellarians.

*The juvenile/adult, sensory receptors*

Two species of Aspidogastrea in particular, *Multicotyle purvisi* from Malayan turtles, and *Lobatostoma manteri* from Australian marine fish, were examined using light microscopy, as well as scanning and electron-microscopy. It is important to understand that juveniles of Aspidogastrea from the intermediate host infective to the final host differ little from adults; either stage will therefore give identical results. Rohde (1966, 1968a), based on the examination under the light microscope of serial sections impregnated with silver, drew attention to the great variety of sensory receptors and their great numbers in *Multicotyle purvisi*. Subsequently, numerous studies also using scanning and transmission electron-microscopy, confirmed this not only for *Multicotyle*, but for *Lobatostoma* as well.

*Scanning electron-microscopy.*

This technique shows only surface receptors (Figure 14). Rohde (1973) counted the surface receptors on scanning electron-micrographs of one specimen of *Lobatostoma manteri* supplemented by counts of another specimen impregnated with silver, and reported numbers as follows: in each anterior marginal alveolus 35, in each marginal alveolus in middle of body 50 (total in all 60 marginal alveoli 2700, in all 29 median alveoli 870); in a marginal row of papillae just dorsal to the alveoli 780; on dorsal part of body 1200, along ventral margins of ventral head lobes 1600, on anterior side of median dorsal head lobe 140, on anterior side of ventral head lobes 300, on anterior sides of lateral dorsal head lobes 300, on posterior side of dorsal head lobes 200, on posterior side of ventral head lobe 150, on neck 200. The overall total is 8440.

Receptors close to the surface form only a small proportion of receptors, the total number therefore is far greater. Considering this, Rohde (1989) estimated that a fully grown worm of this species (4 mm length, unpressed) has a total of 20,000-40,000 receptors, which appears to be extraordinary for a worm of such a small size.

<Figure 14 here>

*Transmission electron-microscopy.*

Transmission electron-microscopy is not restricted to the surface, but can be used to examine interior structures as well. Comparison of serial ultrathin sections has shown that juvenile/adult *Lobatostoma manteri* has at least 8 and possibly up to 14 types of receptors (Rohde, 1989a, 1989b) distinguished by the presence or absence of a cilium and its length, by the absence or presence of ciliary rootlets and their shape, by the number of axonemal microtubules in the axoneme of the cilium, and whether they are part of a complex organ or not. Juvenile/adult *Multicotyle* have 7 and possibly up to 9 types. We illustrate a few major types of *L. manteri* in the following by single sections, although for distinguishing different receptor types, in all cases serial sections were used. All receptors represent differentiated endings of dendrites (nerve fibres), usually with ciliary structures within them. For example, the receptor illustrated in Figure 15 has a short cilium at the end of the dendrite, which is embedded in the surface layer of the worm's surface layer, its tegument. Typically, cilia have a 9+2 structure of the axoneme, i.e. it contains nine pairs (doublets) of microtubules in the periphery and two single microtubules in the centre, but there may be deviations from this pattern. Figure 16 shows a receptor without a free cilium, in which the rootlet is widened to form a large disk. The receptor in Figure 17 has a branched ciliary rootlet.

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Electron-microscopic studies of *Multicotyle purvisi* (1990) have shown the following receptor types, in many respects similar to those of *Lobatostoma*, but differing in some aspects:

- 1) disk-like receptor with many dense collars and a modified ciliary rootlet forming a disk;
- 2) non-ciliate receptor with long rootlet;
- 3) non-ciliate receptor with branching rootlet and dense mass of irregularly arranged microtubules;
- 4) non-ciliate receptor with rootlet fanning out from basal body, cross-striated in its upper and with electron-dense structures in its lower part;
- 5) uniciliate receptor with thick layer of cytoplasm around its axoneme;
- 6) receptor with short cilium, at base of deep invagination of tegument;
- 7) receptor with short cilium terminating in an electron-denser apical cap;
- 8) uniciliate receptor with long cilium.

In addition, there may be a small non-ciliate receptor with a long ciliary rootlet at the base of the thick dorsal tegument, and uniciliate receptors differing from the uniciliate receptor with a long cilium in the number of dense collars and the length of the cilium and ciliary rootlet.

#### *The juvenile/adult, nervous system*

The nervous system of larval and adult *Multicotyle purvisi* was reconstructed in detail using serial sections impregnated with silver, supplemented by sections stained with various other stains, among them some specific for neurosecretion (Rohde 1968c, 1971b, review in (Rohde, 1972). In most Platyhelminthes, the nervous system consists of longitudinal nerves (connectives) connected by transverse nerves (commissures); the dorsal part of one of the most anterior

commissures is often particularly well developed, forming the cerebral commissure or brain. In *Multicotyle*, the number of anterior connectives is much greater than in any other species of the many turbellarians that have been examined, and there are two rings of commissures, one close to the tegument, the other deeper in the tissue. The dorsal part of an interior commissure just anterior to the pharynx is very large, forming the brain (Figure 18). More posteriorly, the nerves form a typical system of connectives and commissures (with one pair of dorsal, one pair of lateral and one pair of ventral connectives), as well as a complex pattern innervating the ventral (adhesive) disk (Figure 19).

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Interestingly, a dense network of nerve fibres (nerve plexus) innervates the intestine (Figure 20), and also the connective tissue septum separating the dorsal part of the body from the ventral disk. Transmission electron-microscopy of the nerves of *Multicotyle purvisi* revealed the presence of a nerve sheath around parts of a posterior connective (Rohde, 1970), a structure not known from other flatworms.

<Figure 20 here>

#### *The larva, sensory receptors and nervous system*

Sensory receptors of larvae of *Multicotyle purvisi* and *Lobatostoma manteri* were examined in several papers (Rohde and Watson, 1990a, 1990b, 1990c, 1990d, 1992b, reviews in Rohde, 1994, 1999). In the former species, altogether 13 receptor types were found, including a paired eye and a paired receptor complex dorsal to the mouth cavity, each complex consisting of two dendrites, one forming a large liquid filled cavity with at least 10 short cilia lacking ciliary rootlets but possessing basal bodies and lamellate extensions of the ciliary membrane, the other

penetrating the anterior wall of the cavity formed by the first dendrite and possessing a single cilium, star-shaped in cross section (Figure 21). Each eye (ocellus) consists of one pigment cell and two receptor cells with rhabdomeres (the light-sensitive dendritic endings, Figures 21 and 22).

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The larva of *Lobatostoma manteri* has only about nine types of receptors: eyes are lacking, and anterior receptor complexes were not found, either. The difference between the two larvae can be explained by the way of how they infect the intermediate host. The latter species in a does not hatch, it is ingested by a snail, the former hatches, swims in water, is attracted to the surface layer by light stimuli, and is then inhaled by a snail host.

The nervous system of larval *Multicotyle* was reconstructed using serial sections impregnated with silver. It shows the basic pattern also found in the adult, with nerves innervating the pharynx, intestine and posterior sucker, and a large number of anterior connectives (Rohde, 1971b).

### ***Infection process and localisation in host, functional morphology***

As discussed above, the two species of Aspidogastrea examined in detail possess some intriguing differences both in morphology and life cycles. The larva of *Multicotyle purvisi* has a larger variety of sensory receptors than that of *Lobatostoma manteri*, including a pair of eyes and an anterior paired receptor complex which are absent in the latter species. It also has ten ciliary tufts and a coat of microfila, i.e. very thin processes of the tegument. The larva of *Lobatostoma manteri*, on the other hand, has a well developed pseudosucker absent in the former species. – Adults of *Multicotyle purvisi* reach a length of at least 10mm (unpressed), of *Lobatostoma*

*manteri* of about 7mm (pressed) and 4mm (unpressed). The former species has a uterus coiled up in the anterior part of the body, with relatively few eggs, the latter species has a uterus filling most of the body, with a large number of eggs. The juvenile and adult of both species have a large number of marginal organs (terminal parts of glands) between the marginal alveoli of the adhesive disk. – In the following I try to explain these differences by differences in the biology, i.e. the life cycles of the species.

*Multicotyle purvisi, infection process and localisation in intermediate host*

Rohde (1971a) described the infection process of *Multicotyle purvisi* from the stomach and occasionally the anterior part of the duodenum of several species of Malayan turtles, with freshwater snails as intermediate hosts, as follows:

Eggs containing embryos at the 1-3 cell stage are laid. Larvae develop in the egg after it has escaped in the feces of turtles into freshwater. In experiments at temperatures of 27-29 ° C first hatching occurred 25 days after egg laying, at 21-28 ° C first hatching occurred after 35-40 days, at 19-22 ° C after 103 days. Environmental temperatures in Malaya are 21-32 ° C (in the shade, lowlands). The hatching process takes only a few minutes. Hatching in cultures under normal diurnal fluctuations of light and temperatures occurs, with few exceptions, in the early hours of the morning. In cultures kept in the dark beyond the normal time of hatching, hatching occurred only after illumination. However, when cultures were kept in the dark over days, hatching occurred also without a light stimulus. – Immediately after hatching, larvae swim with usually extended anterior end, rotating around their longitudinal axis, either along the bottom or straight upwards to the surface, but also irregularly in all directions in the water. They often remain attached to the surface, slowly rotating, or sink slowly to the bottom with the posterior end directed downwards, or faster with the anterior end directed downwards. Larvae can also float in

the middle of the water column rotating slowly around their longitudinal axis, carried sideways by water currents. It sometimes remains at the bottom, appearing to “touch and feel” the substratum. – Larvae are positively phototactic and survived at 26-30 ° C for 5 to over 33 hours. They reach the host less by their own movements, but rather by water currents produced by snails, which carries them into the inhaling opening.

Localisation of larvae in the snails was determined in three specimens of the snail *Pila scutata*: 50 and 69 days, respectively, after infection, a larva was found in the anterior kidney chamber, 108 days after infection, a larva was found in the posterior kidney chamber of the snail. – Experiments showed that turtles become infected by ingesting infected snails. – The smallest specimens of *Multicoyle* found in a large number of naturally infected turtles had 17 and 18 transverse rows of alveoli, respectively. It therefore seems that specimens must be of a certain minimum size before they become infective. Fully grown up and mature specimens have 50 transverse rows of alveoli.

*Functional morphology.*

These features of the life cycle suggest that the larval eyes are responsible for phototaxis which keeps them in the water column where they can encounter snails, but they may also contribute to hatching in the morning. The paired anterior sensory complex may have the function of a balancing organ, as suggested by the ciliary structure extending into interior liquid filled cavities. The coat of microfila increases the surface area without increasing the weight, suggesting that it makes floating in the water column more effective. Ciliary tufts are necessary for swimming, which leads the larvae not directly to the snails, but into the water column where snails may inhale them. This kind of infection behavior is possible only because the habitat of these freshwater snails is relatively undisturbed, i.e. eggs and larvae after hatching do not run a great

risk of being swept away into a less favorable site by adverse currents. The numerous sensory receptors may enable the parasite to keep damage to the very delicate tissues of the host, in particular their kidneys, on which it depends for survival, at a minimum. But they may also contribute to finding the snails' habitat, and to mate finding. – The uterus of the adult can be kept relatively short, because larvae in the eggs develop only after leaving the worm.

*Lobatostoma manteri, infection process and localisation in intermediate host*

Rohde (1973, 1975) described the infection process of *Lobatostoma manteri* as follows: Eggs are laid which contain already fully developed larvae. Snails become infected by eating eggs containing larvae. In experiments, larvae hatched in the stomach of snails (*Planaxis sulcatus* and *Cerithium moniliferum*) and migrated immediately along the ducts of the digestive gland into the digestive follicles.

*Tissue reactions.*

Larvae of *Lobatostoma* feed on secretion and probably epithelial cells of the follicles of the digestive gland of snails. The posterior sucker and developing ventral disk are used for adhesion to the epithelium, and they contribute to its erosion. In heavy experimental infections, 47-49 and 65-66 days after infection, only small parts of the epithelium are still secretory, and the larvae live in large fused cavities. Juveniles are usually found in a cavity formed by an enlargement of the main duct and one or more (?) side ducts of the digestive gland near the stomach in *Cerithium moniliferum*, or in the stomach and main ducts of the digestive gland of *Peristernia australiensis*. They may creep from the ducts into the stomach and back into the ducts. Fish become infected by eating snails.

Rohde and Sandland (1973) examined histological sections of *Cerithium moniliferum* and *Peristernia australiensis* infected with *Lobatostoma manteri*. In the former species (much

smaller than the latter), a single parasite is usually present, coiled up in a cavity formed by the main and one or perhaps some side ducts of the digestive gland, causing metaplasia of the duct epithelium, hyperplasia of the inter-follicular connective tissue and an increase in the number of amoebocytes, and necrosis of some glandular follicles. The latter species may harbor up to six parasites in the stomach and in the large ducts of the digestive gland, with a thickening of the subepithelial connective tissue layer.

Some stages of pathogenesis caused by larval and growing *Lobatostoma* are illustrated in Figures 23, 24, 25, 26, and 27. Note in particular that in the small snail species infected, *Cerithium moniliferum*, a single large juvenile worm is usually located in the digestive gland, in which only a few digestive follicles remain functional (Figure 27), whereas in the much larger *Peristernia australiensis* several large juveniles are often found in the stomach, with tissue reactions around it but most glandular follicles functional (Figures 25 and 26).

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The illustrations show the considerable damage done to the hosts by the infection, although it should be pointed out that naturally infected snails never had as many parasites as experimentally infected ones. Reasons may be that snails in their natural habitat never encounter so many eggs, that heavily infected snails die, or that in natural infections later infections are suppressed by larvae or juveniles already present, either by predation of large on smaller larvae, or by tissue reactions induced by older parasites.

*Functional morphology.*

In view of the pathological findings, it seems reasonable to assume that one function of the variety and number of sensory receptors may be to limit damage done to the delicate host tissue by the parasites. However, they may also play a role in mate finding. Rohde (1973) discussed the adaptive value of the ventral disk: it could be an adaptation for locomotion in or on the soft tissues of the host (snails), perhaps facilitating adhesion of only small portions to a small area of the host's tissue and preventing damage to it. Observations of digeneans and *Multicotyle* and *Lobatostoma* showed that the ventral disk is not more effective for attachment to the vertebrate intestine than the suckers of digeneans, suggesting that it is indeed an adaptation to life in molluscs. It is also very rarely used for tight attachment to the surface of containers or snails. The secretion produced by the marginal glands on the disks has not been examined, but it may be digestive, contributing to the erosion of the digestive gland follicles of the snails, as seen in histological sections. The long uterus of *Lobatostoma* is necessary, because eggs leave the worm only after larvae infective to snails have developed in them. This is necessary because the habitat is rather "violent," exposed to strong tidal currents, and may dry out at low tide, making rapid ingestion of eggs by snails essential.

**Ecology**

*Infection dynamics*

At Heron Island, prevalence of infection of several snail species with various Digenea and *Lobatostoma* was monitored around the island over an extended period (Rohde, 1981). Only snails of the species *Cerithium moniliferum*, *Peristernia australiensis* and *Planaxis sulcatus* were found to be infected with *Lobatostoma*; the aspidogastrid and 11 species of larval digeneans were found in *Cerithium moniliferum* (Rohde and Sandland, 1973), the second species did not harbor

any digeneans. Except for a few exceptions, *Lobatostoma* was found only in a small part of Shark Bay with a flat bottom formed by beachrock, and on beachrock close to it, possibly carried there by snails that had acquired their infection in Shark Bay (Figure 28) (Rohde, 2013).

Examination of beachrock in Shark Bay showed a large number of shell fragments, mainly of *Cerithium*, on it. Netting in Shark Bay yielded small Snubnosed dart, *Trachinotus blochi* (Figures 9 and 10). Its name is derived from the strongly developed muscles in the forehead which move the large pharyngeal plates, an adaptation to crushing the very thick shell of snails. Dissection of these fish revealed *Lobatostoma* in the small intestine and shell fragments in the stomach. Other fish caught in Shark Bay without this structure were never infected. – From January 1971 to April 1972, there was a strong decrease in the relative number of infected snails. During the period of high frequency of infection, *Cerithium* infected with Digenea contained *Lobatostoma* relatively more frequently than snails without Digenea. Snails with double infections disappeared first. Infection with *Lobatostoma* did not affect the relative number of egg producing *Cerithium* during the period of high frequency of infection. – *Lobatostoma* from fish with single infections produced eggs with the haploid number of seven chromosomes and development did not proceed beyond the blastula stage (Rohde, 1973).

<Figure 28 here>

***Populations/communities in equilibrium or non-equilibrium? A demographic or autecological explanation?***

There has been much debate about how common equilibrium conditions, largely determined by competition, are in ecological populations and communities. Here we attempt to interpret the findings on *Lobatostoma* using two ecological paradigms. Walter and Hengeveld (2000, also Hengeveld and Walter, 1999) distinguished the demographic and autecological paradigms. In the

former, species are thought to be demographically similar but have different functions in communities. Intra- and interspecific competition have great importance, leading to coevolution by optimisation processes (i.e. processes that bring about optimal adaptation to environmental conditions), to saturation of communities with species, and to equilibrium. Optimisation is thought to be possible over short time spans because the abiotic environmental component is, on average, constant. - According to the autecological paradigm, species are dissimilar entities affected by abiotic and demographic factors; optimisation is impossible because of the greatly variable environment. The demographic paradigm asks: why do so many species share the same resources; the autecological paradigm asks: how did species arise and how do they survive in a variable and heterogeneous environment; it focuses on the unique nature of adaptations and on species with their spatial responses to environmental conditions. Walter and Hengeveld claim that the two paradigms are mutually exclusive.

We ask which of the two paradigms is better suited to explain the unique adaptations of the two aspidogastreans discussed, and the distribution of *Lobatostoma*. As pointed out above, the Aspidogastrea are a very ancient group, having diverged from the digenean trematodes more than 400 million years ago. Its unique features (adhesive disk, marginal glands, great variety and number of sensory receptors, no multiplication of larvae in the intermediate host) also are likely to be very ancient. It is unlikely that they have evolved as short-term adaptations to particular environments. – Possible competitors with the two aspidogastreans are larval Digenea in the snails. However, the distribution of *Lobatostoma* and Digenea at Heron Island clearly shows that prevalence of infection with Digenea is greatest in a small habitat which also has the heaviest infections with *Lobatostoma*, making it unlikely that interspecific competition plays any role in determining the distribution of *Lobatostoma* at Heron Island. Intraspecific competition, i.e.

competition between individuals of *Lobatostoma* in the snails, may well occur, as suggested by the observation that the smallest of the three snail species infected, *Cerithium moniliferum*, very rarely contains more than one juvenile of *Lobatostoma*. More individuals simply cannot be accommodated (Figure 27). But it is difficult to see how this could have led to any of the adaptations and to the distribution of the species. Clearly, each species has features that are long-term adaptations to a particular kind of life cycle and habitat. In other words, only the autecological paradigm can explain them.

Caution is, however, necessary in accepting the statement that the two paradigms are mutually exclusive. Rohde (2005), in discussing the relative frequency of equilibrium (caused by competition) and non-equilibrium conditions in biological systems, stressed that groups with certain characteristics will tend to exist in equilibrium, others will tend to exist in non-equilibrium. Both conditions are possible and depend on the size of populations and individuals, and on the vagility of the species. If all these are small (as in the aspidogastreae), a tendency towards non-equilibrium results (Rohde, 2005).

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